

Fitting Models of the Population Consequences of Acoustic Disturbance to Data from Marine Mammal Populations

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LONG TERM GOALS

To build an ecological modeling framework that facilitates understanding of the at-sea condition and health of various species of marine mammals. We will use the results from these models to explore and quantify the impact of different types of disturbance (both environmental and anthropogenic) on these species. Modeling will be within a Bayesian framework, which will allow us to fully account for uncertainty in the data, the biological processes, and in model output.

OBJECTIVES

Our scientific objectives are to build a statistical framework for understanding the at-sea health of (initially) three species of marine mammals: southern and northern elephant seals, and northern right whales.

For elephant seals our goal is to build a hierarchical Bayesian model that provides daily estimates of lipid status, as lipid status of the mother is directly linked to pup survival (McMahon et al. 2000). This model will use the drift dive behavior of elephant seals (Crocker et al. 1997) as the link to the underlying true, yet immeasurable, lipid state.

For right whales, our scientific objective is to build a model that provides spatially and temporally explicit estimates of individual health, movement, and survival. The model builds upon some of the ideas from the elephant seal project, but as the photo-identification of individual right whales is the core of the data, the model also includes many ideas concerning mark/recapture from (Clark et al. 2005)

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APPROACH

Jim Clark leads work on the PCAD project at Duke University with the assistance of one Postdoctoral Researcher, Rob Schick. For the past year, the work has focused on fitting the elephant seal drift dive/lipid status model to an expanded data set of both species, and exploring several scientific hypotheses.

Together with colleagues from the PCAD working group, we have finished the analysis, written a manuscript, and submitted it for publication. We have submitted the manuscript twice: first to *Ecology Letters*, and, following that, to *PLoS Biology*. We have reformatted the introduction, and parts of the discussion sections to broaden the scope of the message. We submitted this revised version to *Ecology* this week.

We have also spent considerable time formulating and building the right whale model. Initially we used simulated data as part of the model building process as there were some data sharing issues that needed to be sorted out. When these issues were behind us, and once we had access to the data, we began to assimilate the full set of real data. (In order to get access to the data, we wrote an official data proposal/request to the Right Whale Consortium – the main working group of researchers in the right whale community that govern access to the survey and photo-id data.)

We are currently writing the right whale model formulation and data assimilation process, and will submit this manuscript to a statistical journal. Following this, we will work closely with Dr. Roz Rolland and Amy Knowlton of the New England Aquarium to write separate manuscripts that focus on a) individual health, and b) individual and population level survival as a function of entanglement and propeller scarring.

In addition to active work on these models, both Clark and Schick have participated in two PCAD working group meetings in 2011 (April in the Bahamas, and June in Boston, MA). The meeting in June was hosted and sponsored by ONR/PCAD and was comprised of most of the prominent and active members of the Right Whale Consortium. Clark and Schick each gave presentations to this sub-working group on the model formulation, and the data assimilation. The main goal of this meeting was to engender goodwill with the community and come up with a structure for moving forward with several different analyses.

We have presented the work to external audiences in a variety of venues. Schick traveled to the AESS meeting in Burlington, VT in late June and gave three presentations (in addition to his own, one each on behalf of Len Thomas, and David Lusseau). Schick traveled to Austin, TX to present the right whale model at ESA. The presentations at both conferences were included as part of PCAD sponsored and organized symposia. In September, Schick presented the elephant seal work at the ESOMM conference in Amsterdam, and gave the departmental seminar at CREEM, University of St. Andrews, where he discussed both the elephant seal work and the right whale work.

Elephant Seals

We detailed the research approach in last year's report. Before examining results, we briefly recap it here. The state-space model for at-sea lipid gain/loss in elephant seals contains two primary

components: an observation model for the drift dives, and a process model for the lipid gain/loss process experienced at sea. The observation model is:

$$D_{i,t} \sim N\left(\alpha_1 + \alpha_2 \frac{L_{i,t}}{R_{i,t}}, \frac{\tau^2}{h_{i,t}}\right),$$

where $D_{i,t}$ is the observed mean daily drift rate (in m/s) of individual i , α are the parameters governing the link between lipid status and drift, $L_{i,t}$ is the estimated daily lipid status of individual i (in kg), $R_{i,t}$ is the fixed daily lean mass value of individual i (in kg), and $h_{i,t}$ represents the number of drift dives. This means the observation error decreases with an increasing number of drift dives.

The process model for lipid gain over time depends on the environment, individual differences, and model error,

$$\prod_{i=1}^n \prod_{t=1}^T N_+\left(L_{i,t} | L_{i,t-1} + x_{i,t-1}\beta + w_{i,t-1}\gamma_i, \sigma^2\right) \\ \gamma_i \sim N(0, G)$$

Lipid content at $t+1$ is conditioned upon lipid content at time t and the environment. The truncated normal density $N_+(\cdot)$ has non-negative values for positive $L_{i,t}$ and zero otherwise. Environmental covariates are contained in the 1 by p design vector $x_{i,t}$ a subset of which are included as $q < p$ random effects $w_{i,t}$ (Clark 2007). Population level parameters β and random individual effects relate covariates to lipid gain.

In summary, the model provides estimates of the lipids time series (L), the regression parameters that govern lipid gain/loss (β), missing covariate data (X), the α parameters governing the link between the lipid/lean ratio and the observed drift rate ($D_{i,t}$), the observation error $\left(\frac{\tau^2}{h_{i,t}}\right)$, and the process error (σ^2).

Research Questions

We structured our manuscript around three scientific hypotheses: 1) changes in lipid reserves are a function of individual and environmental covariates; 2) changes in body condition depend on foraging strategy; and 3) females with low lipid reserves at departure preferentially put on lean tissue during the initial phase of a foraging trip.

Elephant Seals - Fitting the Model to Data

Following methods outlined in (Clark 2007), we fit the model to data as follows. We 1) initialize the L and R time series for each animal, 2) setup the design matrix containing the covariates governing change in lipid, 3) set the prior distributions, and 4) initialize each of the MCMC chains. The Gibbs sampler allows us to factor the above high dimensional model into a series of lower dimension

conditional distributions. At each step through the Gibbs sampler, we sample new values for each parameter conditioned on all other parameters, as well as the current value of the parameter being estimated (Clark 2007). Using this approach over many steps through the Gibbs sampler we build up the marginal posterior distribution for each of the parameters or quantities to be estimated.

We experimented with a variety of model formulations. Covariates in the model have been both environmental and individual. An example of an environmental covariate would include a remotely sensed ice cover value for each day, while for an individual covariate an example would include mean daily surface transit. We experimented with many different model formulations, and used model selection an expert opinion to guide our decision of the final “best” model.

To facilitate model selection, we calculate marginal model likelihood for each of these different models (Clark 2007). That is, we tally the likelihood of the data y given the set of parameters θ_m associated with a given model M_m . Given this probability, $p(y | M_m)$, for each model, and a penalty for model size (the model prior), we find the model with the highest posterior probability.

Elephant Seals – The Data

We have successfully fit the above model to two separate datasets for northern and southern elephant seals. There were 29 northern elephant seal tracks and 30 southern elephant seal tracks. Example tracks from each species are shown in *Figure 1* and *Figure 2*.

The final model for northern elephant seals included the following covariates:

- transit
- # of drift dives
- lipid/lean ratio
- foraging strategy (Pelagic, Northeast Pacific, or Coastal)

The final model for southern elephant seals was similar with the added detail that each foraging strategy (Ross Sea, Shelf, Pelagic) was subset temporally based on three phases, i.e. transit away from the colony, foraging, and transit back to the colony. For example the Ross Sea strategy goes from one state two three: Ross Sea-transit away, Ross Sea-Foraging, and Ross Sea-return.

Right Whales – Initial Summary

We were slowed somewhat late last fall following the PCAD meeting in Woods Hole and the Right Whale Consortium meeting in New Bedford, as the data-sharing protocols needed to be worked out. We met with Scott Kraus and Doug Nowacek in Durham, NC early in January and agreed on the way forward.

Subsequent to that meeting Clark and Schick wrote an official request to the Right Whale Consortium for access to the right whale data. This was approved in March, and in April we began the process of summarizing and assimilating the data. We made substantial progress on developing the model this summer. A brief description of the modeling approach follows.

Right Whales – Model Summary

Consider a whale i at month t occupying a zone $z_{i,t} = k \in \{1, \dots, K\}$ characterized by age $a_{i,t}$ and health status $h_{i,t} > 0$. A live individual thus is defined by state vector $[z, a, h]_{i,t}$. Depending on its health status and differential mortality risk posed by, say, boat traffic that could differ between zones k , the individual survives $s_{ik,t} = 1$ to month $t+1$ with probability $q_{ik,t}$. During this month ($t, t+1$) it may remain in k with probability m_{kk} or move to zone l with probability m_{lk} . Using the sighting and health status evidence we wish to infer the impact of age and previous health status on current health and the effect of health and the differential risk associated with zones on survival. The time of death T_i is typically unknown, but is known in some cases. When time of death is known, age of death A_i could be known if age of birth is known. Month t is the number of months since the beginning of modeling, January 1970.

The number of sightings of individual i in zone k in month t is

$$\prod_{i=1}^n \prod_{t=t_i}^{T_i} \prod_{k=1}^K \text{Pois}(y_{ik,t} | \lambda_i E_{k,t})^{I(z_{i,t}=k)}$$

where t_i and T_i are the imputed birth and death months, $z_{i,t}$ is the location of i in month t , $E_{k,t}$ is the search effort in zone k in month t , and the λ_i is the expected number of sightings per unit effort for individual i . $z_{i,t}$ is known for individuals and months where there are sightings ($y_{ik,t} > 0$), and it is imputed for other individuals and months.

Health status observations are ordinal on discrete space $H_{i,t} \in \{1, 2, 3\}$, originally declining from highest to lowest health status. We inverted the scale to match the underlying latent health state increasing from zero, $h_{i,t} > 0$ and range up to approximately 100. The observation model is

$$\begin{aligned} H_{i,t} &\sim \text{multinom}(1, \eta_{i,t}) \\ \text{logit}(\eta_{i,t,1}) &= \ln\left(\frac{\eta_{i,t,1}}{\eta_{i,t,2} + \eta_{i,t,3}}\right) = c_{01} + c_{11}h_{i,t} \\ \text{logit}(\eta_{i,t,1} + \eta_{i,t,2}) &= \ln\left(\frac{\eta_{i,t,1} + \eta_{i,t,2}}{\eta_{i,t,3}}\right) = c_{02} + c_{12}h_{i,t} \\ \eta_{i,t,3} &= 1 - \eta_{i,t,1} - \eta_{i,t,2} \end{aligned}$$

where there is a vector of probabilities associated with each of the health classes $\eta_{i,t} = (\eta_{i,t,1}, \eta_{i,t,2}, \eta_{i,t,3})$

and four fitted coefficients $c = \begin{bmatrix} c_{01} & c_{11} \\ c_{02} & c_{22} \end{bmatrix}$

that translate the continuous scale for h to the ordinal scale for H .

Initially the only information we had for health was the body fat code developed by Roz Rolland (Pettis et al. 2004). However this summer we received additional measures of health from New England Aquarium. This included rake marks (on the left and right side), cyamids on the blow holes, and skin condition. All of these new indices were structured similarly to the body fat code, and as such we developed a similar assimilation function that translated discrete observations into continuous health (*Figure 3*). Finally, we also received the entanglement data from Amy Knowlton at NEAq, and an example time series for one animal highlights both body fat code, and entanglement episodes (*Figure 4*).

Individual health is a latent state

$$N(h_{i,t} | w_{i,t-1} \alpha, \sigma^2)$$

where a is the vector of fitted coefficients, and the design vector $w_{i,t-1} = \begin{bmatrix} 1 & h_{i,t-1} & a_{i,t-1} & a_{i,t-1}^2 \end{bmatrix}$ includes an intercept, an AR(1) term for temporal coherence in health, and age terms to allow for that fact that survival probabilities initially increase ($a_3 \geq 0$) but can eventually decline with age ($a_4 \leq 0$).

The probability of survival from t to $t+1$ is

$$\begin{aligned} \Pr(s_{ik,t} = 1) &= \text{Bernoulli}(\theta_{ik,t}) \\ \text{logit}(\theta_{ik,t}) &= x_{ik,t} \beta \\ x_{ik,t} &= \begin{bmatrix} h_{i,t} & z_{i,t} \end{bmatrix} \end{aligned}$$

where the design vector contains health status and a fixed effect for the zone, and the vector of coefficients has length $1 + K$. Priors are positive for health and non-informative for zone.

Location is sometimes known and sometimes imputed. Let $z_{i,t}$ indicate a zone occupied by i in month t and

$$u_{ik,t} = I(z_{i,t} = k)$$

be the occupancy vector indicating the event that i is in k at t . If the individual is observed in k at t , then $y_{ik,t} > 0$, $u_{ik,t} = 1$, and $u_{i(k' \neq k),t} = 0$. The individual may also be in k at times when it is not observed. The event of moving from j to k at some time during month t (between t and $t+1$) is

$$w_{ikj,t} = I(z_{i,t} = j, z_{i,t+1} = k)$$

The probability associated with this event is

$$m_{kj} = \Pr(w_{ikj,t}).$$

WORK COMPLETED

We have completed the following tasks:

1. Built the statistical model to estimate at-sea lipid status in elephant seals
2. Tested the model using simulated data
3. Fit the model to southern elephant seals
4. Fit the model to northern elephant seals
5. Sampled static and dynamic covariates for southern and northern elephant seals
6. Wrote and submitted the elephant seal manuscript to *Ecology*
7. Finished data exploration for northern right whales
8. Finished data assimilation for northern right whales
9. Built the initial statistical model for right whales
10. Fit the model to data and begun to explore areas where more biological input is needed
11. Presented the results at 4 different conferences/seminars
12. Established a relationship with the primary right whale researchers for current and future collaborations in this modeling effort

RESULTS

Elephant Seals – Results

The primary results from the model are the daily estimates of individual lipid content. We are concerned with the times and places in which animals gain and lose lipids. We are also interested in whether the lipid gain/loss process differs as a function of foraging strategy. We display these in a novel way with a plot type (termed a “horizon” plot) that allows for visually discerning gain/loss and magnitude of a time series over time.

The gain/loss process in the two species differs dramatically (*Figure 5, Figure 6*).

Elephant Seals – Summary

We have quantified the different ways in which elephant seals gain lipids, highlighting both the inter-species and intra-species differences in this process. We have shown how foraging strategy in these different species can dramatically (at least in the case of southern elephant seals) alter the way in which animals gain lipids. As part of this we have been able to discern how individuals employing different strategies might be vulnerable to future climate change.

Right Whales – Initial Results

We are still in the early phases of model fitting and refinement, but initial results suggest two things: 1) we need more informed priors on certain aspects of the model – namely movement; and 2) the outputs have the potential to make lasting impacts for right whale conservation.

Example output from the model includes estimates of the effect of the environment on health, and in turn the effect of health survival – at both the population (*Figure 7*) and the individual level (*Figure 8*). It also includes estimates of movement at both the individual (*Figure 8*) and population level (*Figure 9*).

IMPACT/APPLICATION

To date, no one has been able to estimate the at-sea lipid status of foraging seals. Though previous efforts have used the drift dive signal in relation to environmental features (Biuw et al. 2007; Robinson et al. 2010), this is the first attempt to actually estimate the hidden physiological process of lipid gain/loss in pregnant females. Because the link between arriving maternal mass and future juvenile survival is strong (McMahon et al. 2000), this represents a significant advance in our understanding of the at sea physiology of elephant seals.

Finally, and perhaps more importantly, we have shown a new and important approach to analyzing movement data. Specifically using this approach we can now determine where and when animals are acquiring resources. This represents a big advance, and can be used not only in other systems, e.g. any individuals tagged with dTags, but also in the design of new tags that can take advantage of this approach to define new dive-processing algorithms.

For right whales, despite many years of extensive data collection, there have been very few attempts to put all of the different data types together into a coherent modeling framework. While previous efforts have quantified survival in this population (Caswell et al. 1999; Fujiwara and Caswell 2001), these attempts have neither been Bayesian nor spatial.

We feel that within the PCAD project goals, understanding where and when animals do better/worse will represent a significant contribution. Because there are so many known stressors for right whales, if we can provide a framework that quantifies the impacts of these stressors, it should allow for more informed management decisions. In addition, because this approach is Bayesian, it should also allow for more refined answers to research questions as data continue to accrue.

RELATED PROJECTS

None

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Figures

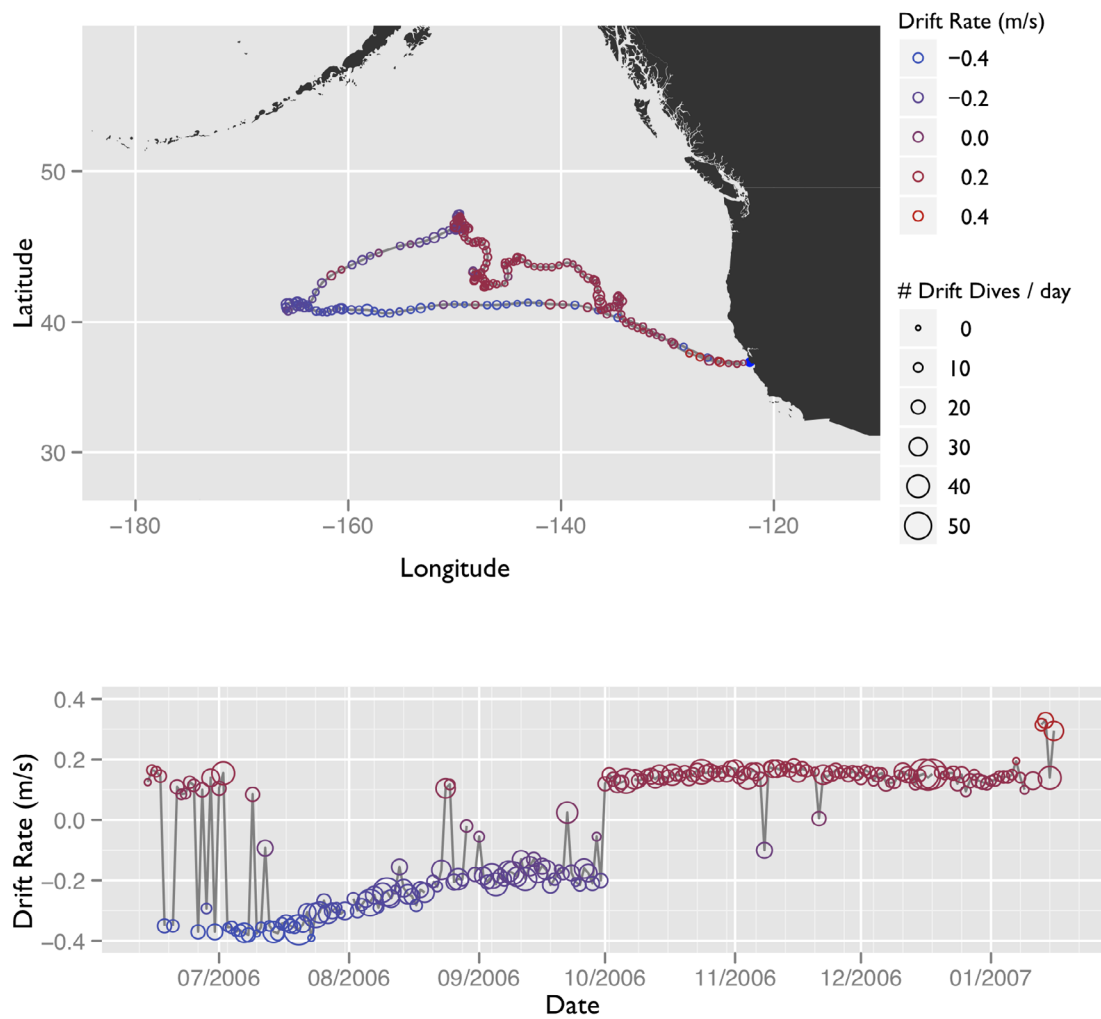


Figure 1. Foraging trip map, and drift rate time series for one Northern elephant seal (M583) tagged at Año Nuevo in 2006. Colors and symbols are the same in each panel. A large shift to positive buoyancy occurs in early October, 2006.

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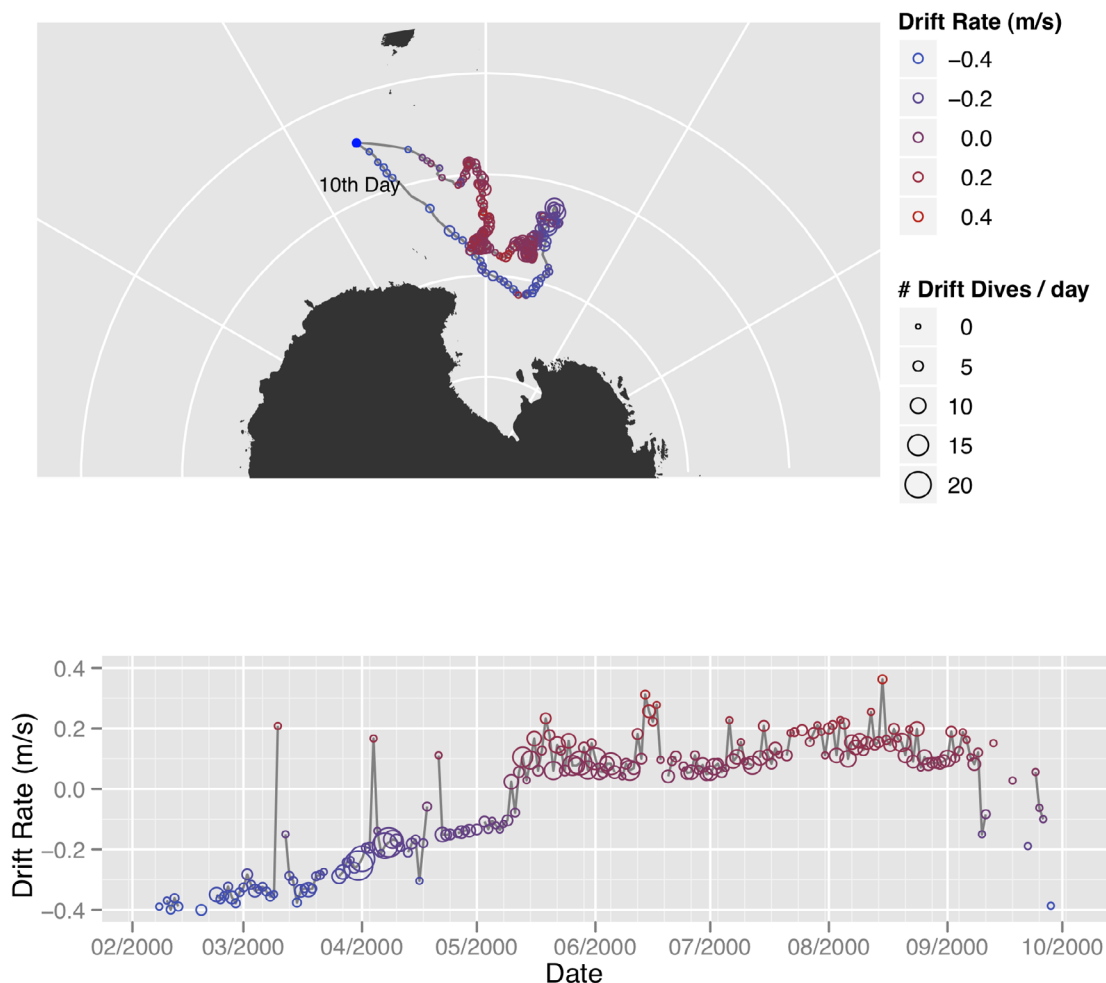


Figure 2. Sample track of one Southern elephant seal tagged in 2000 (b889, post molt). This animal exhibits and ice-edge, or Ross Sea, foraging strategy. She became positively buoyant in early to mid-May, remaining that way until the very end of her foraging trip. For display purposes, the data are projected into an Azimuthal Equidistant projection. Concentric lines of latitude are, from the South pole northward, -80, -70, -60, and -50 °S. Radial lines of longitude are, from left to right, 120 °E, 150 °E, 180 °E, 150 °W, 120 °W.

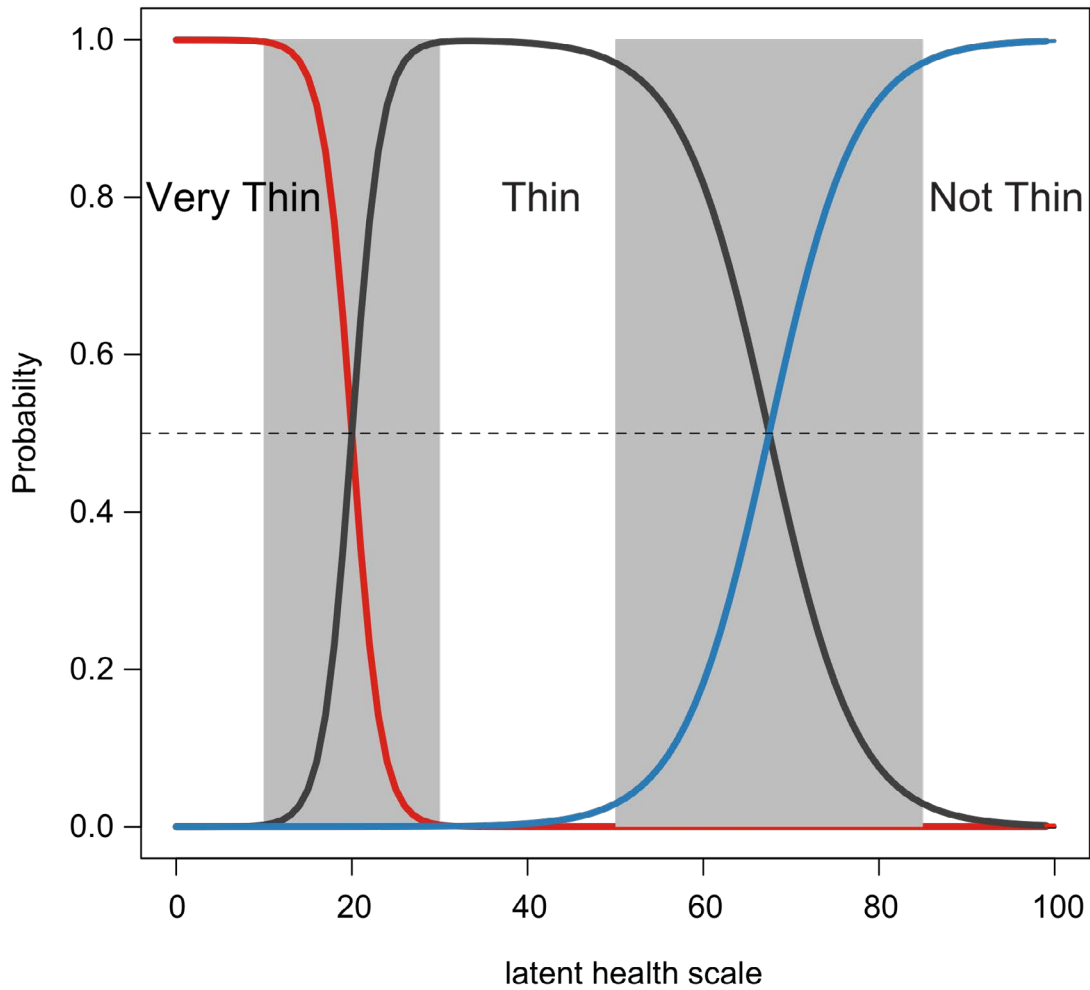


Figure 3. Graphical example depicting how the observations in discrete space, e.g. “very thin,” “thin,” and “not thin” are fit into continuous space. Here we have priors on both the breaks between the different fat classes (depicted by the grey rectangles) as well as the steepness of the decline/overlap between categories. For example, the steepness of the “very thin” category (red line) denotes that there is less uncertainty on your true health given the observation.

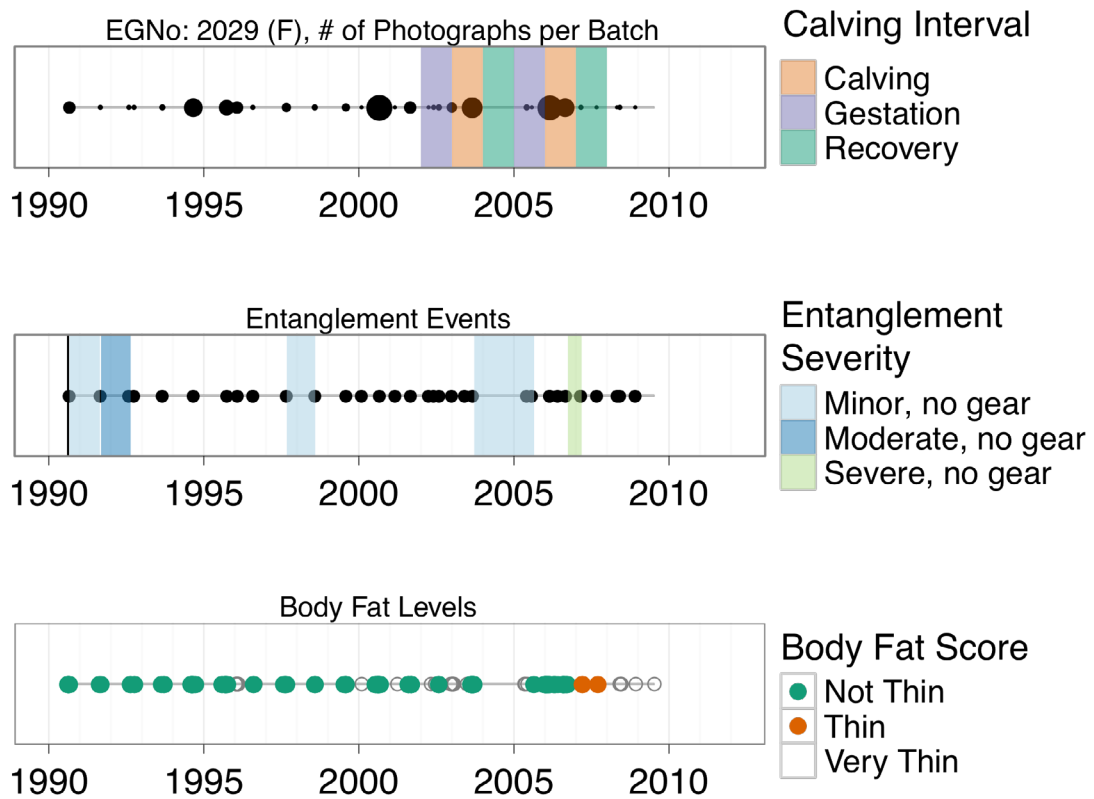


Figure 4. Data time series for one individual EG 2029, now an adult female that has had two calves. The position of the circles in each panel corresponds to sightings of 2029. The size of the circles in the top panel corresponds to the number of photographs taken of the individual within a given time period. Colored rectangles denote the different calving stages, each of which is presumed to have different effects on health – separate from anthropogenic stressors. In the second panel the periods within which the animal is entangled is noted with the colored rectangles; saturation in color denotes whether or not the animal was carrying gear at the time of resighting. Finally the third panel denotes the body fat score assigned to the different sightings periods.

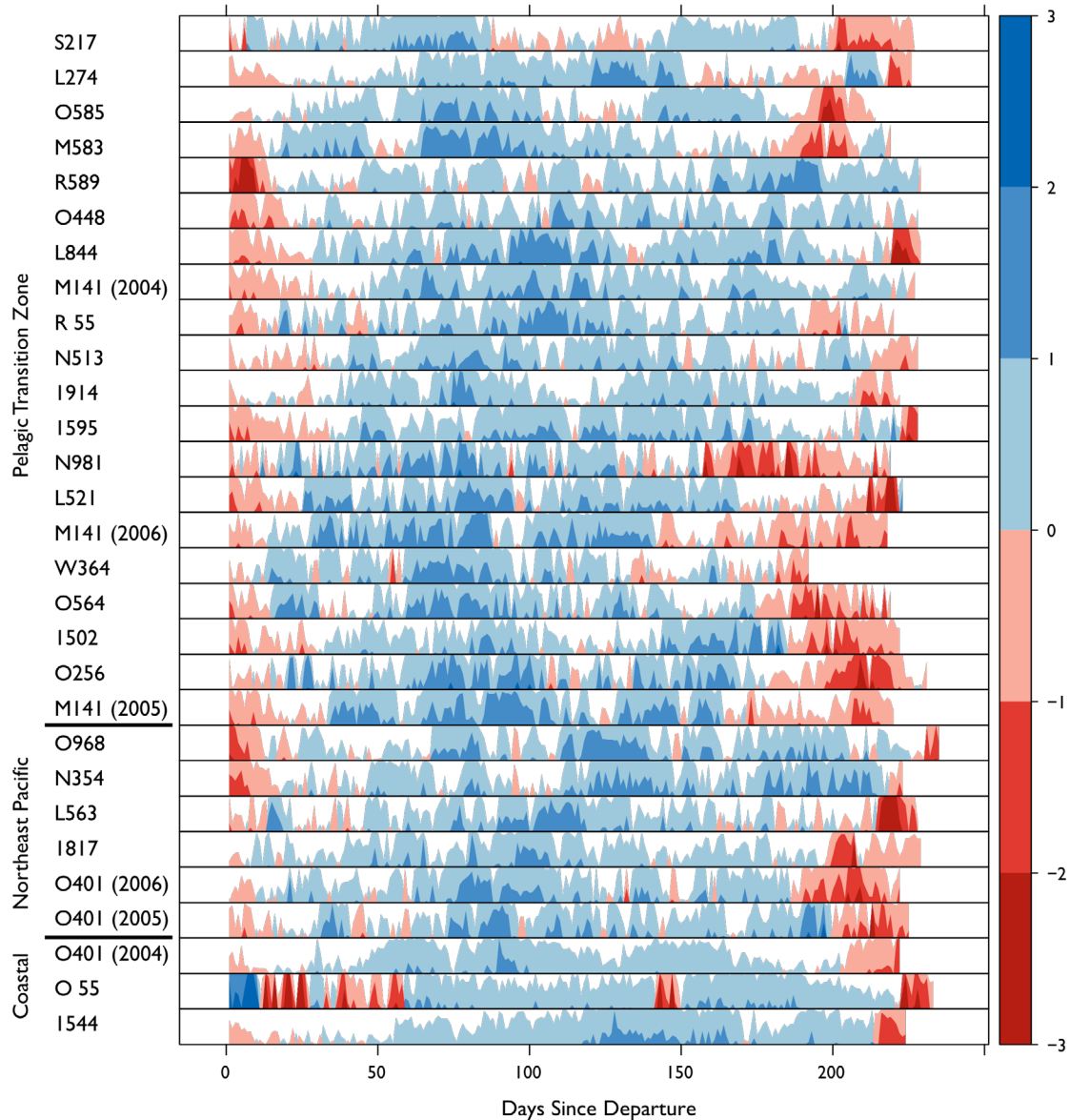


Figure 5. A “horizon plot” (*sensu* Few, 2008) depicting daily lipid gain (blue) and loss (red) over the post-moult foraging trip for 29 northern elephant seals (*Mirounga angustirostris*) from the Año Nuevo colony. This category of plot shows gain and loss as filled areas on the same positive ordinate, with color depicting the direction of the change. The filled areas are sliced into three equal levels (the color bar) with the highest and lowest values of gain and loss shown in the most saturated colors. The magnitude of lipid gain/loss is shown with increasingly saturated colors, and is scaled equivalently across individuals. The three horizontal bars on the left denote which animals use which foraging strategy: 1) pelagic transition zone; 2) Northeast Pacific; and 3) Coastal US/Canada. Within each foraging strategy the animals are ordered based on departure lipid percentage, with leanest animals at the top, fattest animals at the bottom. Animals who employ the coastal strategy put on less lipids than animals employing either the pelagic or North Pacific strategy. Animals with a higher departure lipid percentage upon departure put on lipids faster.

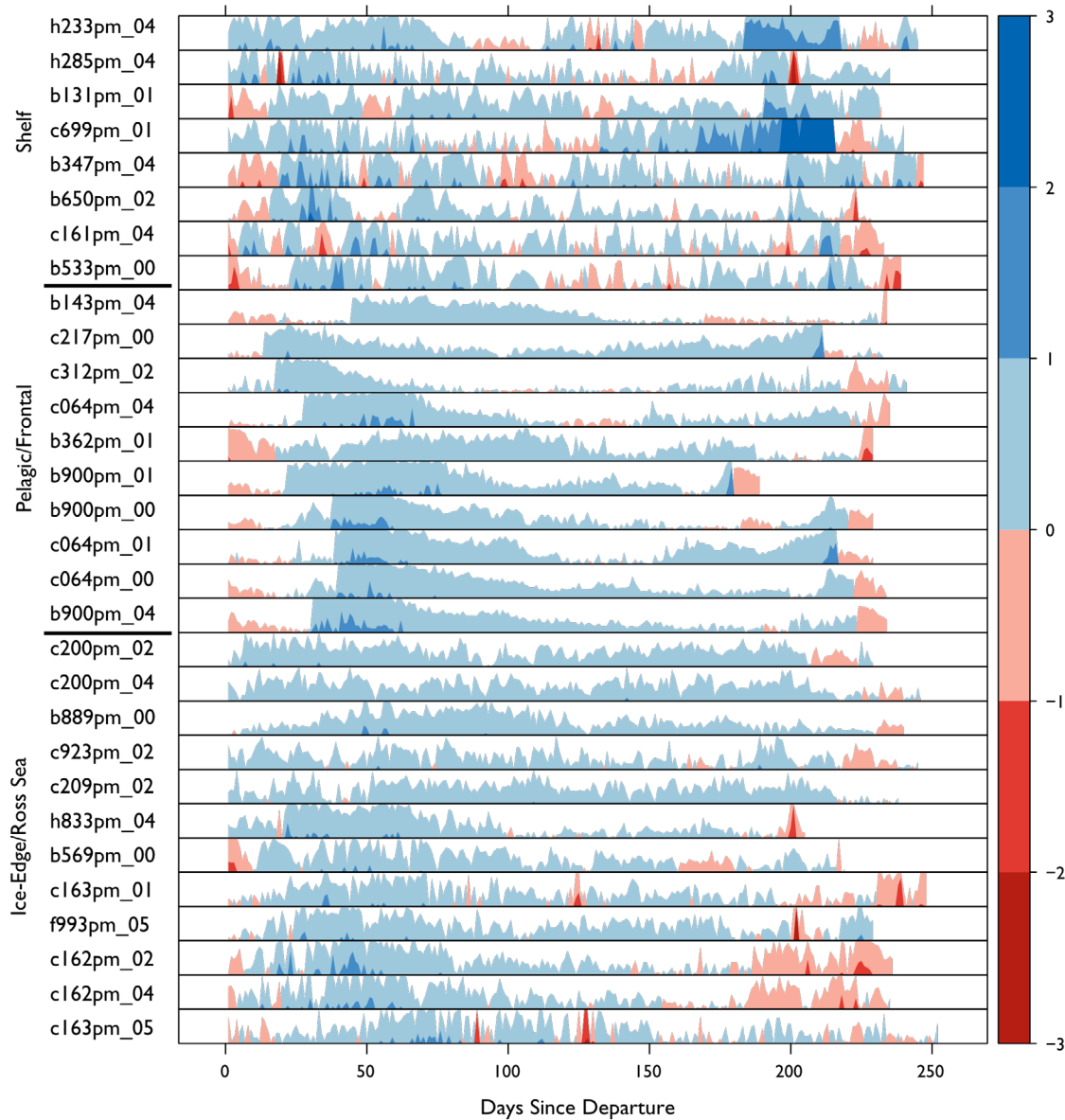


Figure 6. A “horizon plot” as in Figure 3 depicting daily lipid gain (blue) and loss (red) over the post-molt foraging trip for 30 southern elephant seals (*Mirounga leonina*) from the Macquarie Island colony. The three horizontal bars on the left denote which animals use which foraging strategy: 1) animals going to the Antarctic shelf west of the Ross Sea; 2) animals who forage in the pelagic zone to the south and east of Macquarie; and 3) animals that forage in the Ross Sea. Within each foraging strategy the animals are ordered based on departure lipid percentage, with leanest animals at the top, fattest animals at the bottom. Lean shelf associated animals put on lipids for a longer duration than fatter animals employing the same strategy. Pelagic animals range the farthest from the colony, and gain lipids for a sustained period. Ross Sea animals gain throughout their trip, but the gain is much more varied across animals.

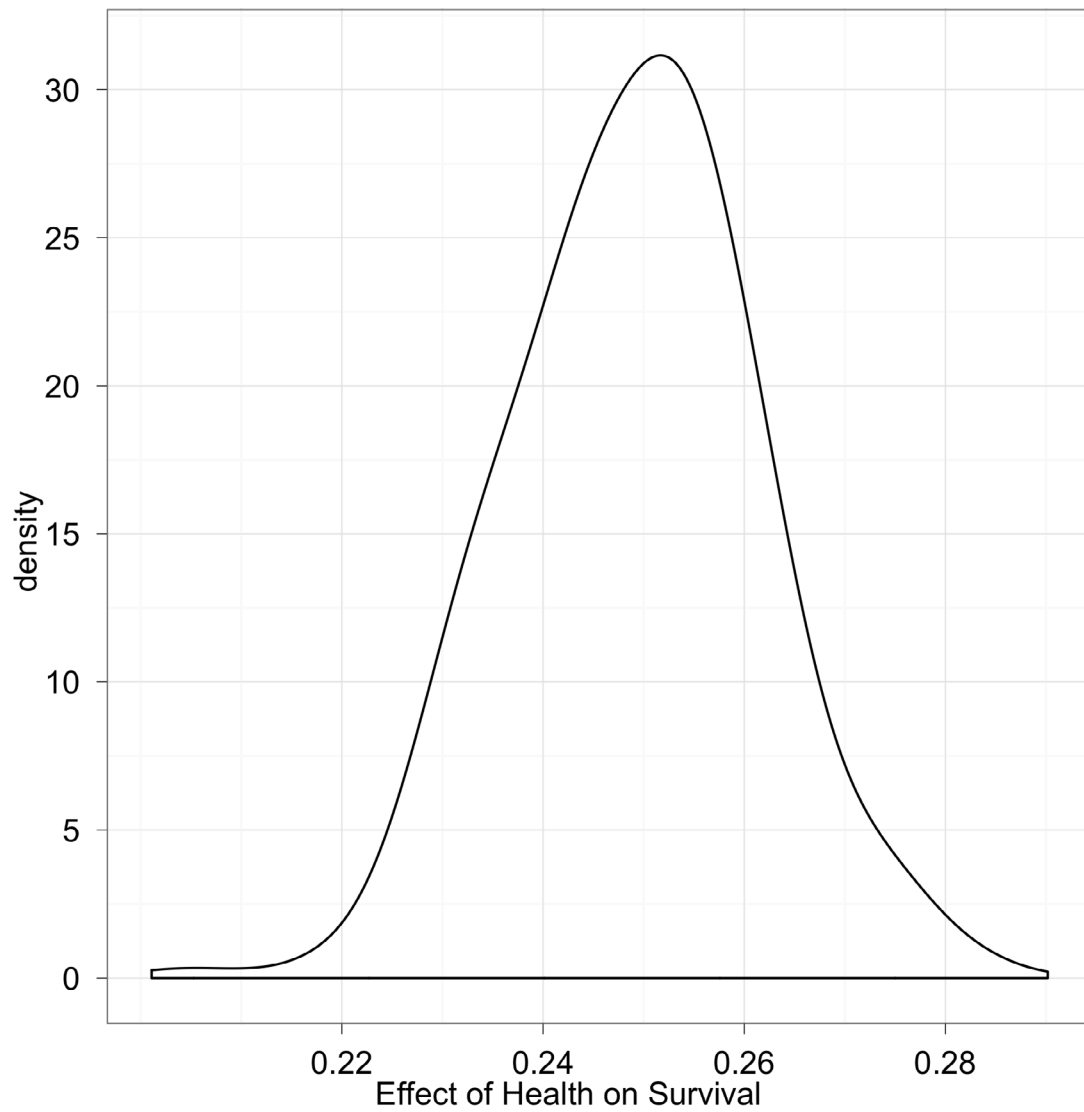


Figure 7. Initial parameter estimate for the effect of health on the survival of the right whale population. See section ‘Right Whales – Model Summary’ for more details on how the model for survival is structured and how the parameters are estimated.

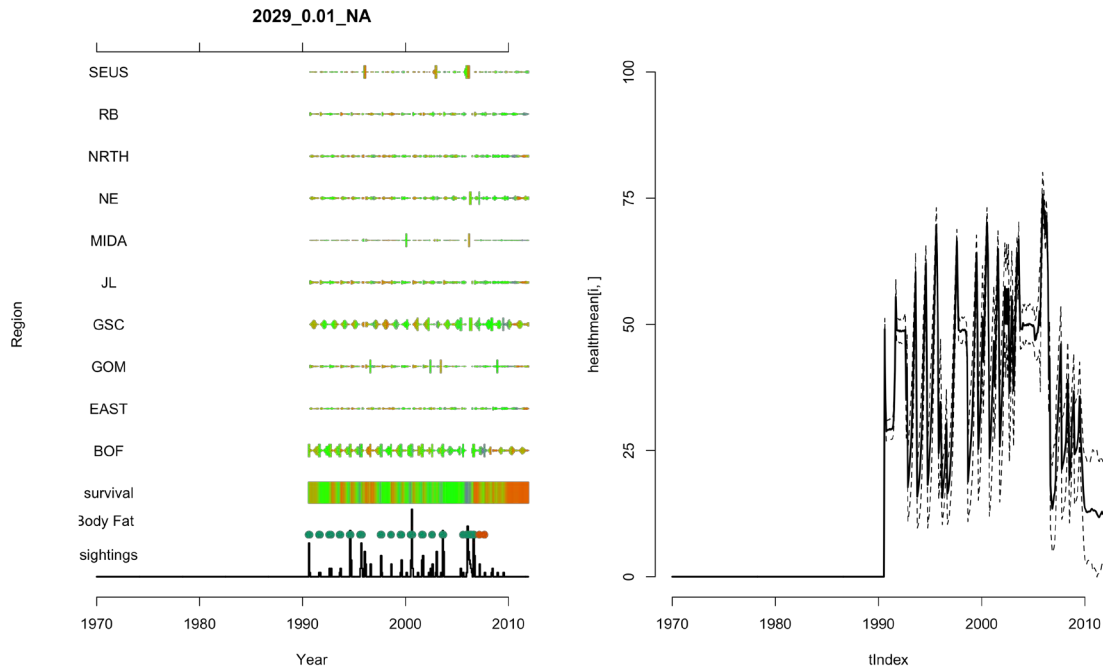


Figure 8. Individual level inference on movement, survival, and health of one right whale – EG 2029 (Figure 4). Horizontal elements in the left panel correspond to the probability of this animal being in any one of the 10 geographic regions in the model. The three additional horizontal elements include the estimate of survival (colored by health), observations of body fat, and number of sightings of this individual. Right hand panel provides an estimate, with uncertainty, of the health of this same animal over time.

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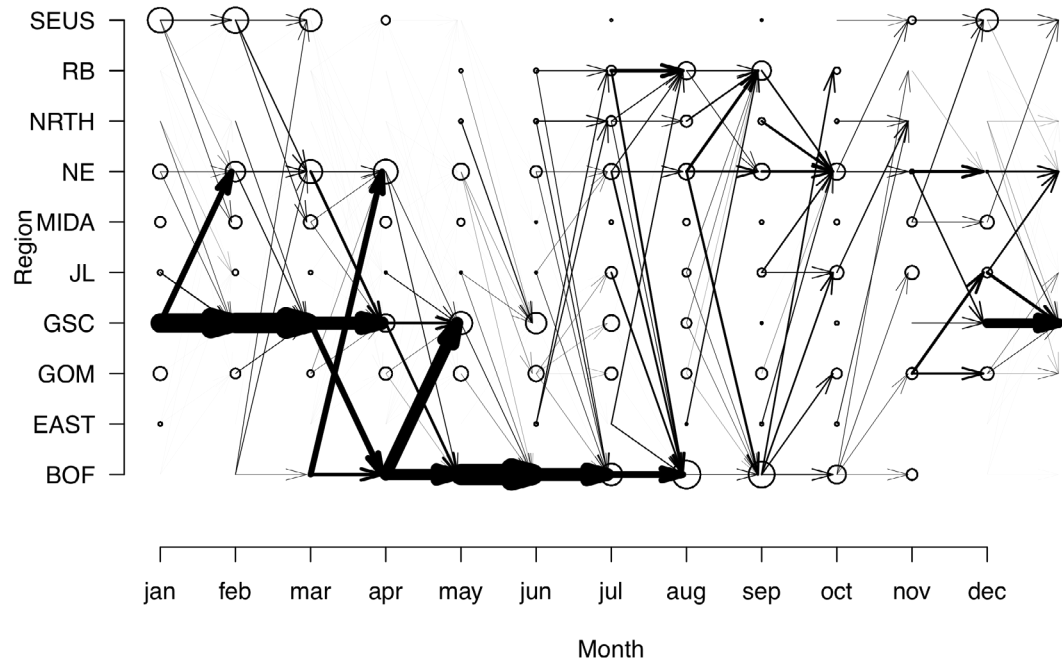


Figure 9. Population level summary for patch residency and movement probabilities for female northern right whales. Size of the circle corresponds to the number of whales seen in that patch/geographic region at any given month, while the direction and thickness of the arrows correspond to patch transitions and the likelihood of such a transition, respectively.